RESEARCH ARTICLE

# The importance of pollination and dispersal syndromes for the conservation of Cerrado Rupestre fragments on ironstone outcrops immersed in an agricultural landscape

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#### **Abstract**

Studies on pollination and seed dispersal are essential for the conservation of plant diversity. In this study, we aimed to evaluate the pollination and dispersal syndromes of five fragments of the Cerrado Rupestre immersed in an agricultural landscape to answer the following questions: (i) What is the frequency of pollination and dispersal syndromes among species and individuals?; (ii) Which are the predominant pollination and seed dispersal syndromes in this environment?. A total of 66 species, belonging to 44 genera and 29 botanical families, were evaluated. Melittophily was the most common type of pollination syndrome, observed in 54.55% of the species, followed by phalenophily (9.09%), cantharophily, ornithophily, quiropterophilly and sphingophily (all 3.03%), and psychophilly (1.51%). Generalist pollination represented 22.73% of the records. Of the 1246 individuals identified, 59.23% were melitophilous, 25.20% generalists, 5.86% phalenophilous, 3.37% quiropterophilous, 2.49% cantharophilous, 2.25% ornithophilous, 1.44% sphingophilous and 0.16% psychophilous. Regarding dispersion syndromes, zoochory was the most common type of dispersion, observed in 68.18% of the species, followed by anemochory (28.79%) and autochory (3.03%). On the other hand, the frequency among individuals differed from the values found for frequency among species. Of the 1246 individuals identified,



55.38% were anemochoric, 43.10% zoochoric, and 1.52% autochoric. Our results demonstrate the predominance of biotic syndromes in the community, especially melittophily and zoochory, contributing to a better understanding of the functionality and availability of resources in the community, as well as indispensable information for the conservation, management, and restoration of natural environments.

#### **Keywords**

anemochory, bees, canga, fruits, melittophily, neotropical savanna, zoochory

#### Introduction

The reproduction in plant species involves many steps, and genetic diversity is influenced by pollinators and dispersers that promote gene flow (Nason et al. 1998). Pollination is a fundamental process in communities, being an essential prerequisite for the reproduction of angiosperms and for the development of fruits and seeds that will be dispersed (Ollerton 2021). It is a mutualistic process of interaction between plants and pollinators, where the partners of this interaction maximize their survival and reproductive success (Ollerton 2021).

Many floral characteristics may reflect adaptive responses to selection by pollinators, that is, some plant species may have characteristic floral phenotypes that are more adapted to more effective or frequent pollinators (Danieli-Silva et al. 2012; Rosas-Guerrero et al. 2014), present more generalized characteristics, influenced by mixtures of pollinators of different functional types, or even present characteristics (i.e. influenced by mixtures of pollinators of different functional types) or floral phenotypes in response to antagonistic insects (Ollerton et al. 2009). Thus, patterns of these plant-pollinator interactions can be characterized as pollination syndromes (Faegri and van der Pijl 1979), which are characterized according to the floral morphology and floral features that attract potential pollinators and the co-evolutionary and interdependent relationship between them (Rosas-Guerrero et al. 2014). Among the main pollination syndromes, we highlight the pollination by wind (anemophily), by birds (ornithophily), by bats (quiropterophilly), by bees (melittophily), beetles (cantharophily), flies (myophily), butterflies (psychophily), sphingids (sphingophily) and moths (phalenophily) (Faegri and van der Pijl 1979).

The frequency of pollination syndromes can vary according to several factors such as vegetation types and their plant strata (e.g., Quirino and Machado 2014; Diogo et al. 2016). Insects, especially bees, are agents present in all plant strata, constituting important pollination resources throughout the entire vertical space occupied by the shrub and arboreal components of forests and savannas (Silva et al. 2012). On the other hand, syndromes such as ornithophily and quiropterophilly, generally occur more frequently on more open edges and formations, perhaps because bats and birds need open spaces to fly (Yamamoto et al. 2007).

After pollination and successful reproduction, plants also adopt different strategies to disperse their fruits and seeds and guarantee seedling survival (Schupp and Fuentes 1995; Wunderlee 1997; Galetti et al. 2013). Plant species have developed several adaptive strategies related to increased dispersal of propagules in response

to associated selective pressure and the highest mortality rate that occurs close to the mother plant. In this way, they can develop mechanisms that allow diaspores to escape conditions that can lead to mortality near the mother plant, where predation, pathogen abundance, and competition are highest (Janzen 1971). However, a more intense seed rain near the mother plant could offset the mortality factors density-dependent, promoting higher recruitment of individuals (Hubbell 1980). Thus, successful dispersal determines the species composition and abundance of a community (Schupp and Fuentes 1995). According to van der Pijl (1982), plants disperse their fruits in three main ways: anemochory, when the diaspore is endowed with structures that provide transport by the wind; autochory, when the plant has its mechanisms for the release of fruits or seeds; and zoochory, whose diaspores have a set of characters that favor dispersion by animals. The latter is characterized by being a more complex syndrome, which, depending on the fauna, is associated with more stable/conserved communities or ones more sensitive to disturbances (Galetti et al. 2013).

The frequency of dispersion syndromes can also vary between different environments (Carvalho 2010; Diogo et al. 2016). In the Neotropics, the proportion of zoochoric species decreases from wet areas to dry areas, where abiotic vectors become more important (Gentry 1982). According to Howe and Smallwood (1982), anemochory predominates in seasonal open canopy environments, such as in the cerrado *sensu stricto*. In this context, it is expected that savanna environments present lower frequencies of zoochoric species than areas of humid forests, where zoochory predominates (Munhoz and Felfili 2005).

Studies on pollination and seed dispersal are essential for the conservation of plant diversity in the tropics and to supply the consumption demands of populations (Resende et al. 2019). Currently, the Cerrado domain comprises the region with the largest agricultural production in Brazil (Lambers et al. 2020). Anthropogenic pressure on this vegetation intensified in the 1970s, contributing to the intense fragmentation of this environment (Morandi et al. 2020). As a result, the remnants of vegetation are restricted to non-farmable areas, such as hilltops, mountain slopes, and some riparian forests (Silveira et al. 2016). Thus, describing the composition of plant species and reproductive biology becomes increasingly essential for the preservation of the remaining areas of the Cerrado and the maintenance of ecosystem services that are so essential for people's health and quality of life (Resende et al. 2019).

In this study, we aimed to evaluate the pollination and dispersal syndromes of five fragments of the Cerrado Rupestre immersed in an agricultural landscape to answer the following questions: (i) What is the frequency of pollination and dispersal syndromes among species and individuals belonging to fragments?; (ii) Which are the predominant pollination and seed dispersal syndromes in this environment? These questions would bring evidence about the interactions between the vegetation community, flower visitors, and seed dispersers who could emphasize the need to preserve the fragmented vegetation. In this way, we approach the patterns of species and individuals of several botanical families through a floristic survey, determining the frequency of pollination and dispersal syndromes among plant species and also among the individuals present in these fragments.

#### Methods

## Study site

The study was carried out in Rio Paranaíba, Minas Gerais, Brazil (19°11'38"S, 46°14'49"W, Fig. 1A), a municipality inserted in the Cerrado Domain, which presents a highly technified agricultural production. The average altitude of the municipality is 1200 m, and the region's climate is classified as Tropical Altitude (Cwa), with two well-defined seasons: the rainy season from October to April, and the dry season from May to September (Alvares et al. 2013).

Five fragments of Cerrado Rupestre were studied, predominantly composed of a continuous crust of canga, also known as "canga couraçada" (Jacobi and Carmo 2008). The types of canga observed in these areas form a rigid layer on the ground, with the roots accessing the soil through cracks or settling in rock crevices (Pereira et al. 2019). All fragments have between 10 and 15 ha, are at an altitude between 1150 and 1250 meters, and are close to the urban area. In addition, as they are located on slopes and hilltops, they are characterized as "Permanent Preservation Areas" (PPAs), representing important remnants of the municipality that persist in agricultural landscapes. The coordinates of the five studied fragments are: fragment  $1 = 19^{\circ}20'55''S$ ,  $46^{\circ}25'81''W$ ; fragment  $2 = 19^{\circ}18'63''S$ ,  $46^{\circ}27'30''W$ ; fragment  $3 = 19^{\circ}18'37''S$ ,  $46^{\circ}25'36''W$ ; fragment  $4 = 19^{\circ}18'65''S$ ,  $46^{\circ}23'62''W$ ; and fragment  $5 = 19^{\circ}16'69''S$ ,  $46^{\circ}22'93''W$  (For more details on these fragments, see Fig. 1B and Pereira et al. 2019).

# Data sampling

In December 2013, 10 random plots of 0.01 ha ( $10 \times 10$  m) were allocated, totaling 0.5 ha in each sampled fragment. (Eisenlohr et al. 2015). All individuals with





**Figure 1.** Geographic location (**A**) and an aerial image of the municipality of the Rio Paranaíba (**B**), Minas Gerais, south-eastern Brazil, showing the five fragments of Cerrado Rupestre studied (image: Google Earth 2021). The fragments evaluated are found on slopes and hilltops, being "Permanent Preservation Areas" (PPAs), and are composed of ferruginous soil that forms a continuous crust known as "canga couraçada".

basal stem diameters (BSD)  $\geq$  3 cm were sampled to obtain species abundance and richness. Dead individuals were not included in our sample. The period of the year (rainy period) did not interfere with the species identification. We identified the species in the field and also had the help of specialists. The nomenclature of the species was according to the species list of the Flora do Brasil (2020).

The life forms of the plant species were classified according to Mendonça et al. (2008). As for pollination syndromes, plant species were classified according to Faegri and van der Pijl (1979): cantharophily, melittophily, ornithophily, phalenophily, psychophilly, quiropterophilly, sphingophily.

Because many species of pollinators can visit the same plant, especially in the absence of resources, the use of pollination syndromes has been the subject of much discussion in the literature, and their use requires caution (Ollerton et al. 2009). However, studies reporting floral syndromes are valid because they indicate that floral evolution is convergent and driven by adaptation to the most effective pollinator group (Danieli-Silva et al. 2012; Rosas-Guerrero et al. 2014). In this way, we classified plant species within specific floral syndromes when the pollinating agents did not vary between the literature consulted or were the most frequent in the pollination of species (thus considered being the main pollinators, see Rosas-Guerrero et al. 2014). However, plant species with floral characteristics that do not fit these classifications and that do not have a main pollinator reported in the literature, being pollinated by several taxons, were classified as generalists.

The types of fruits were classified according to Barroso et al. (1999) and the classification of diaspore dispersion syndromes according to fruit morphology followed the categories proposed by van der Pijl (1982): anemochoric, zoochoric, and autochoric species.

Information about pollination and dispersal syndromes was obtained from the literature (Barroso et al. 1999; Pinheiro and Ribeiro 2001; Gottsberger and Silberbauer-Gottsberger 2006; Kinoshita et al. 2006; Yamamoto et al. 2007; Barbosa and Sazima 2008; Ishara et al. 2008; Kuhlmann and Fagg 2012; Rosas-Guerrero et al. 2014; Kuhlmann and Ribeiro 2016) and in field samples.

# **Data exploration**

We extract frequency data regarding life form, fruit type, pollination and dispersal syndromes, and we build pie charts on these syndromes to explore our data. All analyses were conducted using R base package on R software (R Core Team 2021).

#### Results

A total of 66 species, belonging to 44 genera and 29 botanical families, were evaluated. Regarding life forms, most species studied were trees (57.58%), followed by small trees (25.76%), shrubs (15.15%), and sub-shrubs (1.51%) (Table 1).

**Table 1.** Plant species abundances, life form, fruit type, and pollination and dispersion syndromes at the five fragments of Cerrado Rupestre immersed in an agricultural landscape in Rio Paranaíba, Minas Gerais. N° ind.: number of individuals; cantharophily: beetle pollination; generalist: pollination by many groups of pollinators; melittophily: bee pollination; ornithophily: bird pollination; phalenophily: moth pollination; psychophilly: butterfly pollination; quiropterophilly: bat pollination; sphingophily: hawk moth pollination; anemochory: wind dispersal; autochory: dispersion carried out by the plant itself; zoochory: animal dispersal.

| Family/Species                                  |    | Frag | me | nts (  | n° ir | ıd.)  | Life form | Fruit  | Pollination      | Dispersion  |
|---|----|------|----|--------|-------|-------|-----------|--------|------------------|-------------|
|   | 1  | 2    | 3  | 4      | 5     | Total |           |        |                  |             |
| Annonaceae                                      |    |      |    |        |       |       |           |        |                  |             |
| Annona coriacea Mart.                           | 2  | 0    | 1  | 6      | 1     | 10    | tree      | fleshy | cantharophily    | zoochory    |
| Xylopia sericea A.StHil                         | 0  | 0    | 21 | 0      | 0     | 21    | tree      | fleshy | cantharophily    | zoochory    |
| Apocynaceae                                     |    |      |    |        |       |       |           |        |                  |             |
| Hancornia speciosa Gomes                        | 1  | 11   | 1  | 1      | 0     | 14    | tree      | fleshy | sphingophily     | zoochory    |
| Aspidosperma tomentosum Mart.                   | 1  | 12   | 13 | 17     | 22    | 65    | tree      | dry    | phalenophily     | anemochory  |
| Asteraceae                                      |    |      |    |        |       |       |           |        |                  |             |
| Piptocarpha rotundifolia (Less.) Baker          | 0  | 0    | 0  | 2      | 0     | 2     | subtree   | dry    | psychophily      | anemochor   |
| Bignoniaceae                                    |    |      |    |        |       |       |           | ·      |                  |             |
| Handroanthus ochraceus (Cham.) Mattos           | 0  | 0    | 0  | 1      | 0     | 1     | tree      | dry    | melittophily     | anemochor   |
| Calophyllaceae                                  |    |      |    |        |       |       |           | •      |                  |             |
| Kielmeyera petiolaris Mart.                     | 14 | 0    | 0  | 0      | 14    | 28    | tree      | dry    | melittophily     | anemochor   |
| Caryocaraceae                                   |    |      |    |        |       |       |           | ,      | 1 7              |             |
| Caryocar brasiliense Cambess.                   | 1  | 4    | 0  | 0      | 1     | 6     | tree      | fleshy | quiropterophilly | zoochory    |
| Celastraceae                                    |    |      |    |        |       |       |           | /      | 17               |             |
| Plenckia populnea Reissek                       | 18 | 3    | 4  | 0      | 18    | 43    | tree      | fleshy | melittophily     | zoochory    |
| Chrysobalanaceae                                |    |      |    |        | -     |       |           |        |                  |             |
| Couepia grandiflora (Mart. & Zucc.) Benth.      | 1  | 0    | 0  | 0      | 1     | 2     | tree      | fleshy | phalenophily     | zoochory    |
| Combretaceae                                    | _  |      |    |        | _     | _     |           |        | F7               |             |
| Terminalia argentea Mart.                       | 0  | 0    | 1  | 0      | 0     | 1     | tree      | dry    | generalist       | anemochory  |
| Connaraceae                                     | O  | Ü    | -  | Ü      | O     | •     | tree      | GI )   | generanse        | uncinocitor |
| Connarus suberosus Planch.                      | 1  | 3    | 0  | 2      | 1     | 7     | tree      | fleshy | generalist       | zoochory    |
| Erythroxylaceae                                 | 1  | 3    | U  | 2      | 1     | ,     | tree      | neshy  | generanst        | 200cHory    |
| Erythroxylum campestre A.StHil.                 | 3  | 0    | 0  | 0      | 0     | 3     | subshrub  | flechy | generalist       | zoochory    |
| Erythroxylum daphnites Mart.                    | 78 | 35   | 30 | 38     | 10    | 191   | subtree   | fleshy | generalist       | zoochory    |
| Erythroxylum tortuosum Mart.                    | 13 | 5    | 6  | 10     | 0     | 34    | subtree   | fleshy | generalist       | zoochory    |
| Erythroxylum sp.                                | 0  | 1    | 0  | 0      | 0     | 1     | subtree   | fleshy | generalist       | zoochory    |
| Euphorbiaceae                                   | U  | 1    | U  | U      | U     | 1     | subtree   | neshy  | generanst        | 200cHol y   |
| Pera glabrata (Schott) Poepp. ex Baill.         | 1  | 0    | 0  | 0      | 0     | 1     | tree      | fleshy | generalist       | zoochory    |
| Fabaceae  | 1  | U    | U  | U      | U     | 1     | tice      | neshy  | generanst        | 200cHoi y   |
| Dalbergia miscolobium Benth.                    | 41 | 106  | 02 | 35     | 89    | 363   | tree      | dry    | melittophily     | anemochory  |
| Enterolobium gummiferum (Mart.) J.F.Macbr.      | 2  | 0    | 0  | 0      | 0     | 2     |           | dry    | melittophily     | zoochory    |
|   |    | 0    | 0  | 0      | 0     | 3     | tree      | •      | melittophily     | anemochor   |
| Fabaceae sp.  Machaerium villosum Vogel         | 3  |      | 0  |        | 0     | 9     | tree      | dry    | melittophily     |             |
| 6   | 8  | 0    | 0  | 1<br>0 | 0     |       | tree      | dry    | melittophily     | anemochory  |
| Machaerium opacum                               | 0  | 2    |    | 1      |       | 2     | tree      | dry    |                  | anemochory  |
| Machaerium sp.                                  | 0  |      | 0  |        | 1     | 2     | tree      | dry    | melittophily     | anemochory  |
| Stryphnodendron adstringens (Mart.) Coville     | 8  | 2    | 5  | 3      | 0     | 18    | tree      | dry    | generalist       | zoochory    |
| Lamiaceae                                       | 0  | 0    | 1  | 0      | 1     | 2     | 4         | G1     |                  |             |
| Aegiphila lhotzkiana Cham.                      | 0  | 0    | 1  | 0      | 1     | 2     | tree      | fleshy | melittophily     | zoochory    |
| Lythraceae                                      | 22 |      | 4  | 0      | 1     | 26    | 4         | 1      |                  |             |
| Lafoensia pacari A.StHil.                       | 22 | 1    | 4  | 8      | 1     | 36    | tree      | dry    | quiropterophilly | anemochory  |
| Malpighiaceae                                   | _  | •    | ^  | ^      | ^     | 2     | _1 1      | .1     |                  | 1           |
| Banisteriopsis sp.                              | 3  | 0    | 0  | 0      | 0     | 3     | shrub     | dry    | melittophily     | anemochor   |
| Banisteriopsis malifolia (Nees & Mart.) B.Gates | 0  | 0    | 4  | 2      | 8     | 14    | shrub     | dry    | melittophily     | anemochor   |
| Byrsonima coccolobifolia Kunth                  | 1  | 1    | 0  | 0      | 0     | 2     | tree      | fleshy | melittophily     | zoochory    |
| Byrsonima crassifolia (L.) Kunth                | 4  | 0    | 0  | 0      | 0     | 4     | tree      | fleshy | melittophily     | zoochory    |
| Byrsonima verbascifolia (L.) DC.                | 7  | 0    | 0  | 2      | 0     | 9     | tree      | fleshy | melittophily     | zoochory    |
| Heteropterys byrsonimifolia A.Juss.             | 0  | 9    | 11 | 0      | 0     | 20    | shrub     | dry    | melittophily     | anemochor   |

| Family/Species                             |    | Frag | gme | nts ( | n° iı | ıd.)  | Life form | Fruit   | Pollination  | Dispersion      |
|--|----|------|-----|-------|-------|-------|-----------|---------|--------------|-----------------|
|  | 1  | 2    | 3   | 4     | 5     | Total |           |         |              |                 |
| Byrsonima sp.                              | 1  | 0    | 0   | 0     | 0     | 1     | shrub     | fleshy  | melittophily | zoochory        |
| Melastomataceae                            |    |      |     |       |       |       |           |         |              |                 |
| Miconia albicans (Sw.) Triana              | 3  | 4    | 2   | 6     | 0     | 15    | shrub     | fleshy  | melittophily | zoochory        |
| Miconia sp. 1                              | 6  | 0    | 0   | 0     | 0     | 6     | shrub     | fleshy  | melittophily | zoochory        |
| Miconia sp. 2                              | 1  | 0    | 0   | 0     | 0     | 1     | shrub     | fleshy  | melittophily | zoochory        |
| Meliaceae                                  |    |      |     |       |       |       |           | •       |              |                 |
| Cabralea canjerana (Vell.) Mart.           | 0  | 1    | 0   | 0     | 0     | 1     | tree      | fleshy  | phalenophily | zoochory        |
| Myristicaceae                              |    |      |     |       |       |       |           | •       | 1 ,          | •               |
| Virola sebifera Aubl.                      | 0  | 2    | 14  | 0     | 12    | 28    | tree      | fleshy  | generalist   | zoochory        |
| Myrtaceae                                  |    |      |     |       |       |       |           | •       | C            | ,               |
| Blepharocalyx salicifolius(Kunth) O.Berg   | 0  | 0    | 1   | 0     | 0     | 1     | subtree   | fleshy  | melittophily | zoochory        |
| Eugenia sp. 1                              | 0  | 0    | 5   | 0     | 0     | 5     | subtree   | fleshy  | melittophily | zoochory        |
| Eugenia sp. 2                              | 0  | 1    | 11  | 3     | 4     | 19    | subtree   | fleshy  | melittophily | zoochory        |
| Myrcia lingua (O.Berg) Mattos              | 1  | 0    | 0   | 0     | 0     | 1     | subtree   | fleshy  | melittophily | zoochory        |
| Myrcia splendens (Sw.) DC.                 | 4  | 0    | 14  | 0     | 0     | 18    | subtree   | fleshy  | melittophily | zoochory        |
| Myrcia variabilis DC.                      | 3  | 0    | 0   | 0     | 0     | 3     | subtree   | fleshy  | melittophily | zoochory        |
| Myrcia sp.                                 | 0  | 0    | 0   | 0     | 1     | 1     | subtree   | fleshy  | melittophily | zoochory        |
| Myrtaceae sp. 1                            | 0  | 0    | 0   | 1     | 0     | 1     | subtree   | fleshy  | melittophily | zoochory        |
| Myrtaceae sp. 2                            | 5  | 3    | 0   | 0     | 0     | 8     | subtree   | fleshy  | melittophily | zoochory        |
| Myrtaceae sp. 3                            | 1  | 0    | 0   | 0     | 0     | 1     | subtree   | fleshy  | melittophily | zoochory        |
| Psidium pohlianum O. Berg                  | 0  | 0    | 1   | 0     | 0     | 1     | subtree   | fleshy  | melittophily | zoochory        |
|  | U  | U    | 1   | U     | U     | 1     | Subtree   | nesny   | menttopiniy  | zoochor y       |
| Nyctaginaceae                              | 6  | _    | 0   | 1     | 0     | 12    | tuaa      | flaahrr | ann amaliat  | a o o ala o mar |
| Guapira noxia (Netto) Lundell              | 6  | 5    | 0   | 1     | 0     | 12    | tree      | fleshy  | generalist   | zoochory        |
| Neea theifera Oerst.                       | 1  | 0    | 0   | 0     | 0     | 1     | subtree   | fleshy  | generalist   | zoochory        |
| Ochnaceae                                  | 0  | 0    | 0   | 1     | ^     |       |           | 0 - 1   |              | 1               |
| Ouratea castaneifolia (DC.) Engl.          | 0  | 0    | 0   | 1     | 0     | 1     | subtree   | fleshy  | melittophily | zoochory        |
| Proteaceae                                 |    | 0    |     | •     | •     | 2     |           | 1       | 1 1 1 1 1    | 1               |
| Roupala montana Aubl.                      | 1  | 0    | 1   | 0     | 0     | 2     | tree      | dry     | phalenophily | anemochor       |
| Rubiaceae                                  |    | 2    | 0   | 2     |       | 2.1   | 1 1       | 0 1     | 1.11         | •               |
| Palicourea rigida Kunth                    | 14 | 3    | 0   | 3     | 1     | 21    | shrub     | fleshy  | ornithophily | zoochory        |
| Rudgea viburnoides (Cham.) Benth.          | 2  | 0    | 0   | 0     | 0     | 2     | tree      | fleshy  | generalist   | zoochory        |
| Tocoyena formosa (Cham. & Schltdl.) Schum. | 4  | 0    | 0   | 0     | 0     | 4     | shrub     | fleshy  | sphingophily | zoochory        |
| Rutaceae                                   |    |      |     |       |       |       |           |         |              |                 |
| Spiranthera odoratissima A.StHil.          | 1  | 0    | 0   | 0     | 0     | 1     | tree      | dry     | phalenophily | autochory       |
| Zanthoxylum riedelianum                    | 0  | 0    | 0   | 1     | 0     | 1     | tree      | fleshy  | generalist   | zoochory        |
| Sapotaceae                                 |    |      |     |       |       |       |           |         |              |                 |
| Pouteria ramiflora (Mart.) Radlk.          | 0  | 0    | 2   | 0     | 0     | 2     | tree      | fleshy  | generalist   | zoochory        |
| Pouteria torta (Mart.) Radlk.              | 0  | 0    | 0   | 5     | 7     | 12    | tree      | fleshy  | generalist   | zoochory        |
| Solanaceae                                 |    |      |     |       |       |       |           |         |              |                 |
| Solanum lycocarpum A.StHil.                | 0  | 0    | 0   | 0     | 3     | 3     | shrub     | fleshy  | melittophily | zoochory        |
| Styracaceae                                |    |      |     |       |       |       |           |         |              |                 |
| Styrax ferrugineus Nees & Mart.            | 3  | 0    | 0   | 12    | 0     | 15    | tree      | fleshy  | melittophily | zoochory        |
| Vochysiaceae                               |    |      |     |       |       |       |           |         |              |                 |
| Qualea grandiflora Mart.                   | 1  | 0    | 0   | 0     | 1     | 2     | tree      | dry     | phalenophily | anemocho        |
| Qualea multiflora Mart.                    | 39 | 17   | 46  | 10    | 15    | 127   | tree      | dry     | melittophily | anemocho        |
| Qualea parviflora Mart.                    | 3  | 0    | 0   | 0     | 0     | 3     | tree      | dry     | melittophily | anemocho        |
| Vochysia thyrsoidea Pohl                   | 7  | 0    | 0   | 0     | 0     | 7     | tree      | dry     | ornithophily | anemochoi       |

### **Pollination**

In all life forms, melittophily was the predominant mode of pollination, occurring in 42.11% of trees, 80.00% of shrubs, and 70.59% of small trees. The only sub-shrubs species was melitophilous (Table 1).

Melittophily was the most common type of pollination syndrome, observed in 54.55% of the species, followed by phalenophily (9.09%), cantharophily, ornithophily, quiropterophilly and sphingophily (all 3.03%), and psychophilly (1.51%). Generalist pollination represented 22.73% of the records (Fig. 2A). Bee pollination also predominated among families, being present in 12 families (41.28%) and being exclusive in ten of them (34.48%). Among the families sampled in this study, Rubiaceae and Vochysiaceae presented the highest diversity of syndromes (Table 1).

The frequency of pollination syndromes among individuals differed from the values found for frequency among species. Of the 1246 individuals identified, 59.23% were melitophilous, 25.20% generalists, 5.86% phalenophilous, 3.37% quiropterophilous, 2.49% cantharophilous, 2.25% ornithophilous, 1.44% sphingophilous and 0.16% psychophilous (Fig. 2C). Melittophily was the dominant syndrome among most individuals, predominating in all fragments (Table 1).

## Seed dispersal

In all life forms, zoochory was the predominant dispersal syndrome, occurring in 55.26% of trees, 70.00% of shrubs, and 94.12% of small trees. The only subshrub species was zoochoric. Among the 66 species sampled in the Cerrado Rupestre, 44 species (66.67%) had fleshy fruits, all zoochorous, and 22 species (33.33%) had dry fruits. Species with dry fruits are predominantly anemochoric or autochoric, except for *Enterolobium gummiferum* (Fabales, Fabaceae), which is zoochoric (Table 1).

Zoochory was the most common type of dispersion, observed in 68.18% of the species, followed by anemochory (28.79%) and autochory (3.03%) (Fig. 2B). Furthermore, this dispersion syndrome predominated in all fragments and species of most other families, except for Asteraceae, Bignoniaceae, Calophyllaceae, Combretaceae, Lythraceae, Proteaceae, and Vochysiaceae, composed exclusively of anemochoric species. Among the families sampled in this study, Fabaceae showed the highest diversity of syndromes, with zoochoric, anemochoric, and autochoric species. The Fabaceae and Rutaceae families were the only ones that presented autochoric species (Table 1).

The frequency of dispersion syndromes among individuals differed from the values found for frequency among species. Of the 1246 individuals identified, 55.38% were anemochoric, 43.10% zoochoric and 1.52% autochoric (Fig. 2D). Differences in the frequency of zoochory were observed between individuals in the fragments: this syndrome predominated in fragments 1 and 4, and anemochory in fragments 2, 3 and 5 (Table 1).

Dalbergia miscolobium, melitophilous and anemochoric, was the most abundant plant species with 363 individuals, followed by  $Erythroxyllum\ daphnitis$  (Malpighiales, Erythroxylaceae) (generalist and zoochoric pollination, n = 191) and  $Qualea\ multiflora$  (Myrtales, Vochysiaceae) (melitophilous and anemochoric, n = 127).

Regarding the five fragments, *Dalbergia miscolobium* (Fabales, Fabaceae) was the most abundant species in fragments 2, 3, and 5, while *E. daphnitis* was the most abundant in fragments 1 and 4, in addition to being the most frequent zoochoric species in the Cerrado Rupestre of Rio Paranaíba (Table 1).

#### **Discussion**

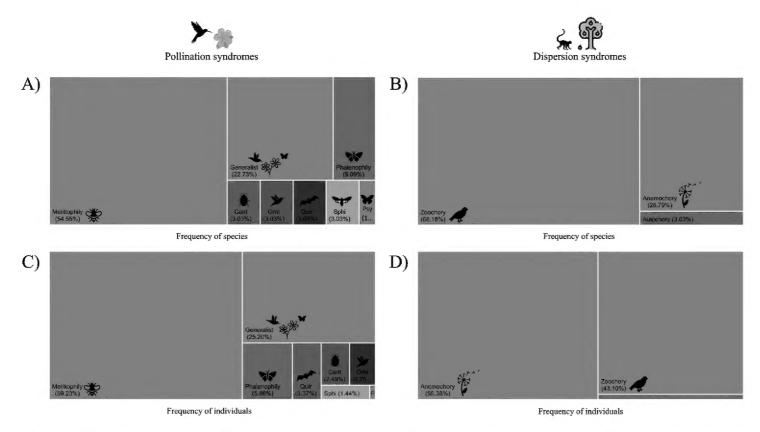
Our results demonstrate the predominance of biotic syndromes in the community, especially melittophily and zoochory, while most individuals, corresponding to species with high dominance, characterize the typical pattern of the predominance of anemochory in this vegetation.

Pollination systems encompassed several groups of animals, being represented by more frequent and less frequent syndromes in these environments. The Cerrado Rupestre studied has a higher frequency of species and individuals potentially pollinated by bees, highlighting the importance of this group of pollinators in the fruiting of most species studied. Bees pollinate about 70% of plants in the Cerrado (Rabeling et al. 2019) and are also the largest pollinators of crops, responsible for increasing the quality and quantity of vegetable seed production, pastures, grains, and fruits (Yamamoto et al. 2010; Patel et al. 2021). This expressiveness is justified by the fact that bees use all resources: pollen, nectar, oil, and resin (Rabeling et al. 2019). Thus, melittophily was the predominant syndrome in several plant families that offered resources such as pollen (for example, Fabaceae, Melastomataceae, and Myrtaceae) and oil (Malpiguiaceae) (Rosas-Guerrero et al. 2014).

The other entomophilic syndromes were less expressive, but many plant species presented a generalized pollination system since their flowers can be pollinated by different generalist pollinators. Even when they are not the main food sources for these insects, the resources offered by these plants can be vital for the persistence of populations of these pollinators in the absence of other sources (Waser et al. 1996; Rabeling et al. 2019). Furthermore, this strategy can compensate for the fruiting of several plants in a possible seasonal insect deficiency (Waser et al. 1996).

On plant communities in the Cerrado, ornithophily and quiropterophilly represent less than 5% of all angiosperm species (Rabeling et al. 2019). These syndromes are strongly related to specific taxa, especially bromeliads (Rocca and Sazima 2010) and cactuses (Cordero-Schmidt et al. 2021), respectively. In the present study, ornithophily was observed in plant species with red or yellow tubular diurnal flowers with large amounts of nectar, on *Palicourea rigida* (Gentianales, Rubiaceae) (see Fig. 3A) and *Vochysia thyrsoidea* (Myrtales, Vochysiaceae). On the other hand, quiropterophilly was associated with *Caryocar brasiliensis* (Malpighiales, Caryocaraceae) and *Lafoensia pacari* (Myrtales, Lythraceae), species with white and yellow flowers of nocturnal anthesis, with a strong odor (characteristic of fermentation).

Regarding the dispersion of diaspores, our results also suggest the importance of fauna for maintaining the diversity of this community, with a predominance of zoochoric species. The highest frequency of zoochoric species observed in the



**Figure 2.** Frequency of pollination (**A**) and dispersal (**B**) syndromes between plant species and individuals (**C** and **D**, respectively) found in the five fragments of Cerrado Rupestre immersed in an agricultural landscape in Rio Paranaíba, Minas Gerais. **A:** Cant = Cantharophily, Orni = Ornithophily, Quir = Quiropterophilly, Sphy = Sphingophily, Psy = Psychophily (1.51%). **C:** P = Psychophily (0.16%). **D:** Green frame = Authocory (1.52%). Cantharophily: beetle pollination; generalist: pollination by many groups of pollinators; melittophily: bee pollination; ornithophily: bird pollination; phalenophily: moth pollination; psychophilly: butterfly pollination; quiropterophilly: bat pollination; sphingophily: hawk moth pollination; anemochory: wind dispersal; autochory: dispersion carried out by the plant itself; zoochory: animal dispersal.

present study (69.6%) was also found in studies carried out in savanna environments (Vieira et al. 2002; Martins et al. 2004; Toppa et al. 2004) and in forest environments (Yamamoto et al. 2007). These results demonstrate that when analyzing the frequency of syndromes among species, there may also be a predominance of zoochory in open environments such as those found in the Cerrado.

The predominance of zoochory may indicate the importance of fauna for plant species in this community. One of the hypotheses to explain the advantages of dispersal by animals is that of colonization and directed dispersal, that is, zoochory allows for the dispersal of larger seeds and, at the same time, it may be more effective than anemochory (Howe and Smallwood 1982; Vander Wall and Longland 2004). Animals commonly move between different habitats, being able to distribute larger amounts of seeds of different plant species. On the other hand, anemochoric and autochoric species depend on random events to disperse their seeds. This unpredictability can cause a smaller number of seeds to be distributed in habitats, or mean that distribution is less effective in distancing themselves from the mother plant (Schupp et al. 2010), despite the advantage of not depending on the availability of biotic agents for dispersion of its diaspores (Howe and Smallwood 1982).

Fleshy fruits, such as berries and drupes (e.g., *E. daphnitis*, second most abundant species in the study, N = 191), are often edible and therefore highly attractive, especially for birds (Fig. 3B), which favors the dispersion (Amico and Aizen 2005; Kuhlmann and Ribeiro 2016). However, dry fruits can also indicate zoochoric dispersion, when they have special mechanisms (Howe and Smallwood 1982; Kuhlmann and Ribeiro 2016), as is the case of the *E. gummiferum* fruit, which is dry and indehiscent, but has a spongy pulp with a strong odor, attracting mammals (Françoso et al. 2014). This wide morphological variation of fruits in the same syndrome reveals the variety of strategies that plants have to attract different dispersers, which, in turn, can benefit from the greater availability of food resources (Valenta and Nevo 2020).

On the other hand, when analyzing the frequency of syndromes among individuals, the predominance of anemochory in the Cerrado Rupestre fragments demonstrates the expected pattern for a seasonal and open environment (Howe and Smallwood 1982; Kuhlmann and Ribeiro 2016). This result shows that abundance is the best indicator of the real availability of resources, such as zoochorous fruits for fauna. This analysis, however, is not commonly done and we suggest with this study that the abundance of species in communities should receive more attention to better understand the distribution of these syndromes in these environments.

The variety of flowers and the availability of fruits in the Cerrado Rupestre, mainly zoochorous, indicate the need for preservation and studies on the degree of dependence of these plants on these animals. Thus, an important next step to be taken is to know the identity of these pollinators and dispersers to understand the role of animal species in the structure of these plant communities (Rabeling et al. 2019; Dellinger 2020; Borchardt et al. 2021). Plant-animal interactions are at the origin and maintenance of diversity and affect the functioning of ecosystems (Fuster and Traveset 2020). Furthermore, the pollination deficit can impact agriculture (Bauer and Wing 2010) and the dynamics of natural systems with variable importance ac-





**Figure 3.** Ornithophily (Bird pollination) and zoochory (animal dispersal) records in the Rupestre Cerrado of Rio Paranaíba, Minas Gerais, Brazil. (A) *Heliomaster squamosus* (Apodiformes, Trochilidae) hummingbird with a beak full of nectar, pollinating a *Palicourea rigida* (Gentianales, Rubiaceae) individual. (B) *Turdus amaurochalinus* (Passeriformes, Turdidae) individual consuming *Erythroxylum suberosum* (Malpighiales, Erythroxylaceae) fruit. Photo credit: Cássio Cardoso Pereira.

cording to the specialization of the interaction (Zamora-Gutierrez et al. 2021). The elimination of disperser animals, on the other hand, can have negative effects on seedling recruitment, and understanding the plant/animal relationship is crucial in conservation programs and reforestation plans (Pérez-Méndez et al. 2016; Török et al. 2020). Therefore, the conservation of fragments of different sizes, as well as the establishment of corridors to connect landscapes, are very important measures to re-establish the animal populations and ensure the continuous regeneration of these communities (Tabarelli and Gascon 2005; Fontúrbel et al. 2017).

#### Conclusion

Anthropogenic pressure on this vegetation is the main threat to pollination and dispersal interactions. Despite the risk, the conservation and management of these fragments can contribute to the maintenance of pollination and dispersal services in the cerrados immersed in agricultural landscapes. Thus, this study provides important data on pollination and dispersal services associated with the Cerrado Rupestre and contributes to a better understanding of the functionality and availability of resources in the community, providing indispensable information for the conservation, management, and restoration of natural environments.

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